Regional and genus-specific factors underpin bleaching variation across India’s corals reefs during the fourth global coral bleaching event

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Abstract

On April 15th 2024 the National Oceanic and Atmospheric Association of the US announced the onset of the fourth global coral bleaching event, coinciding with the 2023-24 El Niño Southern Oscillation. Through a coordinated, nationwide collaboration of scientists, dive centers and citizen observers, we assessed bleaching responses across six reef regions in India, spanning most of the subcontinent's major reef areas, from oceanic atolls and island slopes to mainland fringing and patchy reef formations. While bleaching intensity increased with accumulated heat stress (Degree Heating Weeks or DHW) as expected, it showed distinct regional variability, revealing the limits of DHW as a universal predictor. Among the regions, Lakshadweep was the most affected with severe bleaching even at intermediate DHW. In contrast, Mahatma Gandhi Marine National Park bleached less than other regions, likely reflecting cooling from large amplitude internal waves that could create mesoscale thermal refugia. Across sites, *Acropora*, *Pocillopora*, *Galaxea*, and *Montipora*, were the most affected genera while *Pavona, Platygyra, Goniastrea* and *Favites* were among the least affected. Palk Bay displayed a reversal of canonical genus-level susceptibilities, with only modest bleaching in the normally susceptible *Acropora* colonies, but high mortality in usually resistant *Porites* colonies. These contrasting regional and taxonomic responses highlight how context-specific resistance patterns, and local oceanography mediate thermal stress and underscore the need to integrate these local geographical contexts in our understanding of bleaching impacts on tropical reefs.

Introduction

On April 15th 2024, the National Oceanic and Atmospheric Association of the U.S announced that a mass bleaching event was underway, coinciding with the 2023–2024 El Nino (NOAA 2024). This is the 4th such event in the last 30 years, with the previous three events occurring in 1998, 2010 and 2016 respectively. These mass bleaching events have been unequivocally linked with high thermal anomalies caused by the El Nino Southern Oscillation events (ENSO) (Hughes et al. 2018; Eakin et al. 2022). The heatwaves caused by El Nino events have been increasing in both frequency and intensity over time (Cai et al. 2014; Cetina-Heredia and Allende-Arandía 2023), resulting in a threefold increase in the number of days of marine heat waves per year and over 1 degree rise in their maximum intensity (Marcos et al. 2025). These anomalies add to the steadily rising background rates of ocean warming, triggering bleaching onset earlier as years pass (Reimer et al. 2024). As a result of mass coral bleaching and mortality, coral cover globally has declined by nearly 50% between 1998 and 2018 (Tebbett et al. 2023). This marks an accelerating trend in the coral reef crisis, where the frequency of thermal events increase at intervals faster than the reef's ability to recover from them (Hughes et al. 2018; Dey et al. 2025). This shortening recovery window suggests that coral responses are increasingly conditioned by ecological history as much as by temperature itself.

Predicting where and when large-scale thermally-induced bleaching is likely to occur is challenging. The most commonly used predictive metric is Degree Heating Weeks (DHW), which measures accumulated heat stress at a location by summing up sea surface temperatures that are over one degree above the average maximum summer temperature over a 12-week period (Gleeson and Strong 1995). While it works well at regional levels, there is a significant amount of spatial variability in its predictive power (Liu et al. 2013; Leggat et al. 2022; Whitaker and DeCarlo 2024; da Silva et al. 2025), and some studies suggest that a more context-specific understanding of stressors can better explain bleaching variation (McClanahan et al. 2019).

There are several factors that lead to such bleaching variation, including compositional differences in coral communities with varying thermal tolerances, differential compositions in symbiotic zooxanthellae, differences in microbiomes, lipid reserves, or exposure to prior heat stress events (Baker et al. 2004; Rodrigues and Grottoli 2007; Wagner et al. 2010; Carilli et al. 2012; Palumbi et al. 2014; Cunning and Baker 2020). Environmental factors such as depth, turbidity, and proximity to upwellings may also ameliorate temperature stress, effectively creating thermal refugia at reef scales (Glynn 1996; Chollett and Mumby 2013; Zweifler et al. 2024). Such local processes can generate sharp regional contrasts in bleaching severity even within the same ocean basin. Surveys across large geographical scales can help identify such thermal refugia and increase the efficiency of models aiming to predict the impacts of climate in the future (McClanahan et al. 2020b).

In order to assess the impacts of such events, several independent monitoring efforts have taken place across the globe, resulting in the creation of large global datasets (van Woesik and Kratochwill 2022). However, this data is highly skewed towards a few regions such as the Great Barrier Reef in Australia, parts of Southeast Asia, and the Caribbean (Virgen-Urcelay and Donner 2023; Rivera-Sosa et al. 2025). Given the scale of the disturbance and the lack of comparable data across sites, standardised bleaching assessments are critical from the least studied regions of the world (McClanahan et al. 2020b; Reimer et al. 2024). This is especially important, given the variability in bleaching susceptibility noted by several studies across multiple spatial scales (Arthur 2000; McClanahan 2019; van Woesik et al. 2022; Voolstra et al. 2025).

Studies have documented the impacts of the 2024 Global mass bleaching event from lesser studied regions including the Cayman Islands, Mexico, and Brazil (López-Pérez et al. 2024; Doherty et al. 2025; Mies et al. 2025). However, despite the extensive cover and diversity of reefs across South and South-east Asia - including India - these reefs lack systematic assessments of bleaching events (Reimer et al. 2024; Thinesh et al. 2025). This gap is especially striking given the diversity of India's reef settings, from low-lying atolls and volcanic island slopes to turbid mainland fringing reefs, which together span much of the ecological variation seen across the tropical Indo-Pacific.

Understanding how Indian reefs respond to the 2023–24 El Niño therefore offers critical insight into regional vulnerability and potential resilience. By comparing these contrasting reef types under a common thermal pulse, we explore how geography and community composition interact to shape bleaching outcomes. Although there have been several independent monitoring efforts across several of India's major reefs during past bleaching events, the use of highly variable methods in data collection, and wide spread of surveys over time make comparison between reef sites difficult (Thinesh et al. 2025). Here, we report results from a nationwide collaboration of scientists, dive centres, and citizen observers - the first of its kind in the country - who documented bleaching intensity, heat stress, and genus-specific responses across India's reefs during the 2024 global bleaching event following the same methodology. We evaluated bleaching intensity as a response to heat stress (DHW) and depth at the site, to explore regional and genus-specific patterns in bleaching responses.

Methods

Study Sites

We conducted a rapid bleaching assessment across six reef regions in the Indian sub-continent; namely Lakshadweep, Goa, Palk Bay, Mahatma Gandhi Marine National Park (MGMNP), and Ritchie's archipelago (Fig. 1). These regions represent a longitudinal gradient of over 20 degrees and encompass atoll reefs (Kavaratti), fringing reefs (MGMNP, Ritchie's archipelago, Palk Bay), and patch reefs (Goa). Although both parts of the Andaman and Nicobar archipelago, Ritchie's archipelago and MGMNP were considered separate regions for the purpose of the analysis because of fundamental differences between the two regions. MGMNP consisted of fringing reefs in Tarmugli and Boat islands. It is a marine protected area, has relatively higher turbidity, and is exposed to Long Amplitude Internal Waves (LIAWs) (Wall et al. 2012). Ritchie's archipelago is made up of fringing reefs off Shaheed and Swaraj Dweep. It is characterised by high exposure to tourism, lower turbidity, and is sheltered from LIAWs by South Andaman Island. Palk Bay, located on the South-East tip of the subcontinent, hosts fringing reefs in moderately turbid waters and a long shallow coastal shelf. Goa's patch reef habitats are characterised by high sediment load, and low species diversity. The island representing the Lakshadweep archipelago is Kavaratti. It is a densely populated atoll, with relatively oligotrophic reefs and low turbidity. All surveys were conducted in a one-and-a-half-month window between 20th April and 7th June 2024. Each region was surveyed at multiple sites (between 2 to 8), and each site in turn was surveyed at 1 or more depths (reefs). Cumulatively, our surveys encompassed a total of 24 sites, and 33 reefs (Table S1).

Sampling

At each site, we used NOAA's coral reef watch Degree Heating Weeks dataset to obtain heat stress values (as Degree Heating Weeks) for each site at the time of sampling. We used a standardised photoquadrat methodology to collect data across all regions except Palk Bay. We used 1x1m benthic photoquadrats to assess percentage benthic cover in Lakshadweep, MGMNP, Ritchie's archipelago, and Goa. Photoquadrats were placed at regular intervals at least 5m apart. Each reef had between 11–24 replicate photoquadrats that were used for analysis. In Palk Bay, line intercept transects were used, following methods delineated by English (1994) (n = 3 per site).

Each photoquadrat was then analysed using the software *Image J* to estimate the percentage cover of each benthic category within the quadrat, including algal cover, rubble, sand, crustose coralline algae, coral, and other invertebrates. The category of coral was further divided into 4 health categories; Healthy, Pale, Bleached, and Recently dead (Fig S1). Healthy corals were those that showed no signs of bleaching. Pale coral was those which showed colour loss due to a partial reduction in zooxanthellae density, but still possessed some colour, or displayed protective fluorescence. Bleached coral was identified as being white, and therefore having expelled nearly all zooxanthellae. Recently dead corals were identified as coral skeletons, sometimes covered in settled turf algae, but where the underlying dead corallite structure was still clearly visible and uneroded. All coral health categories were then scaled to the total coral cover within the quadrat to control for differences in absolute coral cover and used for further analysis. Corals were identified to the genus level, and split into 6 growth forms. These included branching, massive, encrusting, foliose, tabular, and solitary.

These response variables were then combined to create a "Bleaching Intensity Index" (henceforth, BII) – a cumulative index for the consequences of the mass bleaching event. The BII was calculated in a manner like McClanahan et al. (2004).

$$BII = (0 \times\ H \pm\ 1 \times\ P \pm\ 2 \times\ B \pm\ 3 \times\ RD) \div 3$$

where H = Proportion of healthy coral, P = Proportion of pale coral; B = Proportion of bleached coral and RD = Proportion of recently dead coral in a quadrat.

Lastly, to explore genus-specific trends in bleaching, BII was calculated for each genus, to get at regional averages per genus. The best (lowest BII) and worst (highest BII) performing genera were then compared across regions to explore consistency in responses.

Statistical analysis

The effects of DHW at the time of sampling, depth, region and branching ratio on the Bleaching Intensity Index were modelled using a beta mixed-effects model with a logit link function using the package GLMMTMB (Brooks et al. 2023) in the software R. The site was added as a random intercept. Branching ratio was defined as the proportion of branching or tabular colonies in a quadrat, and was added to the model because branching and tabular growth forms have been shown to be disproportionately impacted by bleaching events. DHW, Depth and Branching ratio were continuous variables, while Region was a categorical variable with 5 levels. BII was transformed before modelling using Smithson and Verkuilen's (2006) transformation, in order to scale the index such that it fits between one and zero but does not contain ones or zeros.

Depth and DHW were also added as variables to model the dispersion parameter to account for heteroskedastic data.

The model structure was as follows

Bleaching Intensity Index ~ Depth + DHW + Region + Branching_ratio + (1|Site), dispformula = ~ Depth + DHW

Results

Heat stress and Benthic Composition

Temperature stress varied across India's reef regions, with Degree Heating Weeks (DHW) during April-June 2024 ranging from 1.3 to 10.2 DHW, reflecting both differences in sampling times, but also considerable differences in the susceptibility of each geography to heat stress accumulation (Table 1). Sites in Goa, Lakshadweep and MGMNP were surveyed early, under relatively modest heat stress (1–5 DHW), whereas Ritchie's archipelago, Lakshadweep, and Palk Bay were sampled as anomalies intensified (7 to 10 DHW).

Benthic composition varied sharply across reef regions. Average coral cover was highly variable across regions, from 11% cover in Lakshadweep to ~ 58% in MGMNP (Fig S2). Goa's reefs were patchy and corals were interspersed with large sand patches (24% cover). Lakshadweep and Ritchie's archipelago were characterised by high algal cover (algal cover > 50% cover in both regions).

Table 1
The Heat stress at the point of sampling and the maximum heat stress faced by sites within each region during the El Nino of 2023-24. DHW's when sampled was included as a predictor variable in the model

Location	DHW's when sampled	Maximum DHW for 2024
Lakshadweep	4.27, 7.11	7.74
Goa	1.29, 3	8.41
Palk Bay	6.69	7.92
Ritchie's archipelago	8.51, 8.8, 9.8, 9.81	10.21
MGMNP	4.52, 4.83, 4.92, 4.98	7.6

Bleaching Intensity

Region had a strong effect on BII (Fig. 2a): Lakshadweep exhibited a significantly higher bleaching intensity, while regions such as Goa and MGMNP showed significantly lower BII relative to Lakshadweep (Fig. 2a). Due to collinearity between Region and DHW, the model displays wider confidence intervals and increases the rate of false-negative error, but not false positives. As a result, this may decrease our ability to detect differences between regions, however, where differences are significant, they are likely to be true.

As expected, DHW showed a strong positive effect on BII ($\beta = 0.255$, $p = 0.03$*). Depth had a small but significant negative effect on BII ($\beta = -0.031$, $p = 0.004$*) indicating slightly reduced bleaching at greater depths (Fig. 2c, Table S2a). BII was also more variable at higher temperatures and greater depths, indicated by the significance of both DHW and depth in the dispersion formula of the beta regression (Table S2b). Interestingly, the proportion of branching or tabular coral did not influence BII of coral ($\beta = 0.036$; $p = 0.7$, Fig. 2d, Table S2a).

Genus-specific responses

While different regions experienced different degrees of heat stress, we would expect the rank order of the bleaching intensity of genera within regions to remain similar across regions. Acroporid coral genera such as *Montipora* and *Astreopora*, as well as others such as *Pocillopora* and *Galaxea* were *consistently* among the most affected (with the highest BII values), whereas *Pavona*, *Favites*, *Goniastrea* and *Platygyra* tended to show the lowest BII values where present (Fig. 3).

Several common coral genera including *Porites*, *Acropora, Montastrea* and *Symphyllia* had variable responses across regions. Porites, generally considered a relatively stress-tolerant genus, showed highly variable patterns - bleaching less in MGMNP, but with much stronger bleaching responses in Palk Bay and Lakshadweep. Palk Bay stood out for its reversal of bleaching susceptibilities: branching and tabular *Acropora* colonies bleached minimally, while massive *Porites* suffered high mortality.

Discussion

The responses of India's coral reefs to the 2024 global bleaching event indicates that India's reefs do not behave as a single ecological unit. Our collective survey efforts spanned diverse reef geographies from coral atolls and volcanic islands, to mainland fringing reefs and patchy reef formations. Across these locations, bleaching intensity broadly tracked thermal anomalies, yet the strength of reef responses varied sharply between regions. Although depth had only a weak effect on bleaching intensity, the direction of change (lower BII with increasing depth) suggests modest thermal buffering consistent with earlier work (Glynn 1996; Chollett & Mumby 2013). The lack of association with branching-coral abundance, however, is notable. Branching and tabular forms typically bleach first (Loya et al. 2001; McClanahan et al. 2020); the absence of this pattern here may arise from genus-level variability, or from colony-level acclimatisation within shallow, thermally more resistant assemblages (Thomas et al. 2018, 2019). While these effects were minor compared to regional contrasts, they reinforce the broader pattern that bleaching outcomes are mediated by context as much as by exposure to heat. Genera-specific patterns were also evident across most regions; however, some coral genera differed in their responses between regions. These trends confirm the growing acknowledgement that reef responses to thermal anomalies are shaped as much by geographically contingent factors such as finescale oceanographic processes, community composition and local conditioning as by the immediate magnitude of heat stress (Lenihan et al. 2008; Swain et al. 2017; Safaie et al. 2018; De Falco et al. 2020; McClanahan et al. 2020a). The resulting mosaic of vulnerability across the subcontinent shows that ecological fates can vary considerably across reef regions, with equally varied implications for how we manage their futures.

The differences in response patterns between regions, especially in Lakshadweep, MGMNP (Andaman Archipelago) and Palk Bay (Southern Indian coast) illustrates the diversity of bleaching trajectories. Lakshadweep's reefs had a bleaching response consistently higher than other reefs even at intermediate

DHWs (see Fig. 2). The archipelago has endured repeated bleaching events since 1998, with its windows for recovery progressively shortened (Yadav et al. 2018; Dey et al. 2025). While we would expect this repeated exposure to afford Lakshadweeps reefs some buffering capacity due to symbiont shuffling or selective survival, there may be physiological limits to this buffering capacity that the 2024 event breached (Cunning et al. 2015; Schoepf et al. 2015b). Meanwhile, the reefs of MGMNP, at similarly moderate DHWs, had a milder overall bleaching response in comparison to Lakshadweep (Fig S4 and S5). This is consistent with Large Amplitude Internal Waves (LAIWs) that have been documented in the Andaman Sea (Wall et al. 2012; Brown et al. 2025). LAIW's can create mesoscale refugia for corals by reducing local temperatures by several degrees in nearshore environments (Sheppard 2009; Schmidt et al. 2012; Wall et al. 2015; Wyatt et al. 2020). LAIW's in the Andaman Sea approach from the western aspect (Wall et al. 2012), potentially explaining why the west-facing reefs of MGMNP experienced lower bleaching in comparison to more east-facing locations of Ritchie's archipelago. Goa showed significantly lower bleaching intensity as well. The high turbidity across Goa's reef sites could limit the amount of solar irradiance, therefore reducing bleaching stress. Additionally, Goa's reefs had a unique coral community with most abundant coral genera in Goa being either rare or absent from other regions (Fig. 3), and were dominated by foliose *Turbinaria* and other encrusting coral that are often amongst the most resistant to bleaching. These factors may be responsible for the reduced bleaching intensity in Goa, however, since data from Goa was sampled relatively early during the bleaching event, it is also possible that the more significant effects of bleaching may have appeared in the following months.

Across subcontinental reefs several coral genera responded in a consistent manner, with genera like *Astreopora*, *Montipora*, *Pocillopora*, and *Galaxea* showing uniformly higher bleaching susceptibility (higher BIIs). At the other end, *Pavona*, *Favites*, *Platygyra* and *Goniastrea* - predominantly encrusting and massive colonies, showed consistently lower bleaching responses across all regions they were present in (Fig. 4). However, there were important deviations from these broad patterns. This variability was clearest within ubiquitous genera like *Porites* and *Acropora*, which displayed contrasting susceptibility to thermal stress, sometimes even in geographically adjacent regions. This regional variability in genus-level responses cautions against broad generalising of winners and losers, as intra-genus variability may be high, and cumulative stress and ecological memory reshape the landscape of coral tolerance (Muir et al. 2021; Dey et al. 2025).

If Lakshadweep and MGMNP illustrate thermal saturation and oceanic buffering respectively at regional scales, Palk Bay, off the subcontinental coast, departs from canonical genus-level susceptibility patterns. High mortality in *Porites* and largely unaffected *Acropora* indicate a coral assemblage with varying trajectories of resilience from the norm (Fig S5) (Loya et al. 2001). While the Palk Bay surveys need to be read with some caution because sampling was limited and based on slightly different techniques, similar patterns were observed in Palk Bay during the 2016 global mass bleaching event, with massive forms like *Porites* bleaching disproportionately more compared to corymbose and digitate *Acropora*, which largely escaped bleaching (Krishnan et al. 2018; Sadhukhan et al. 2022). In contrast, another study from the adjacent Gulf of Mannar found the opposite response, where *Acropora* showed high thermal susceptibility in response to the same bleaching event (Edward et al. 2018). There is some evidence of potentially increased resilience in *Acropora* colonies that may be linked to increased prevalence of clade D symbionts within *Acropora* colonies (Thinesh et al. 2019; Hussain et al. 2025). It is unclear whether the increased susceptibility of normally resistant *Porites* in Palk Bay waters is linked to other sublethal stressors in these waters (chronic turbidity, coastal nutrients, etc), or to other temperature-related mechanisms and warrants further investigation. Recent reports indicate that in other areas of Palk Bay, *Porites* colonies may have recovered after severe bleaching (M.B. pers. obs.), indicating that there could be sub-regional variations in this response that need to be examined more closely.

In general, Degree Heating Weeks remains a powerful standard global predictor of bleaching, yet the clear outliers in our dataset underscore its lower explanatory power at regional scales. As reefs are exposed to successive stress events and adaptation histories, their responses diverge from simple thermal thresholds (McClanahan et al 2019). For predictions that are more pertinent to smaller scales, models will need to incorporate local ecological memory, differing community compositions, and local oceanographic factors as important predictors of bleaching response (Wooldridge and Done 2004; Boonnam et al. 2022; Whitaker and DeCarlo 2024). In this view, bleaching risk is not purely a function of accumulated heat but of its geographical characteristics, and where a reef stands in its recovery-disturbance cycle (Jokiel and Brown 2004; Dey et al. 2025). Accurate bleaching prediction, therefore, is not just a problem of getting more accurate temperature profiles but of incorporating local ecological histories into regional models.

The functional consequences of coral bleaching and mortality will differ across geographies. For locations along the Indian coast like Goa and Palk Bay, reefs are more marginal and the decline of reefs could reduce reef associated biodiversity and other ecosystem services like tourism. However, in islands like Ritchie's archipelago and MGMNP, reefs additionally play a critical role in coastal sediment production and beach stability (Perry et al. 2015). At the other extreme, for low-lying atolls like in Lakshadweep, the threats of coral loss are existential, with reducing carbonate accretion and rising sea levels threatening the very habitability of atoll islands (Storlazzi et al. 2018; Divan Patel et al. 2023).

While measuring bleaching impact is useful as a baseline, the eventual consequences of the fourth global bleaching event will only emerge over time with continuous monitoring of post-bleaching mortality, recovery, and community reassembly. Our rapid bleaching monitoring effort inevitably underrepresents spatial and taxonomic diversity. Additionally, the Bleaching Intensity Index condenses complex response trajectories into a single metric that needs to be interpreted with caution. Yet the coordinated framework we adopted across six of India's reef regions demonstrates that national-scale rapid assessments are feasible and can feed urgently needed regional data into global databases. Establishing permanent, standardised monitoring would convert such rapid responses into a longitudinal record of change and resilience.

With four planetary-scale bleaching events in less than thirty years, the declining intervals between disturbances stretch the ability of reefs to recover by removing energy reserves, reducing coral reproductive output, and increasing disease susceptibility (Schoepf et al. 2015a; Muller et al. 2018; Cheung et al. 2021; Leinbach et al. 2021; Briggs et al. 2024). Taken together, the regional differences in our data project India's reefs as a microcosm of the global reef condition - from thermally susceptible atolls and oceanic islands influenced by local physical dynamics, to mainland fringing reefs surviving in turbid marginal environments. The Indian record shows that the next phase of coral-reef change will not be defined solely by global temperature curves but by how local processes including thermal history, hydrodynamics, coral composition, and local resistance interact with them. This nuanced patchwork of responses reflects the spectrum of global reef futures, where locally varying factors determine whether reefs succumb, resist or adapt to repeated thermal stressors. Capturing this diversity of responses will require better prediction, achievable only through sustained observations of each cycle of decline and recovery.

Declarations

Open research policy: Associated data available in Zenodo at https://zenodo.org/records/18115480

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Figures

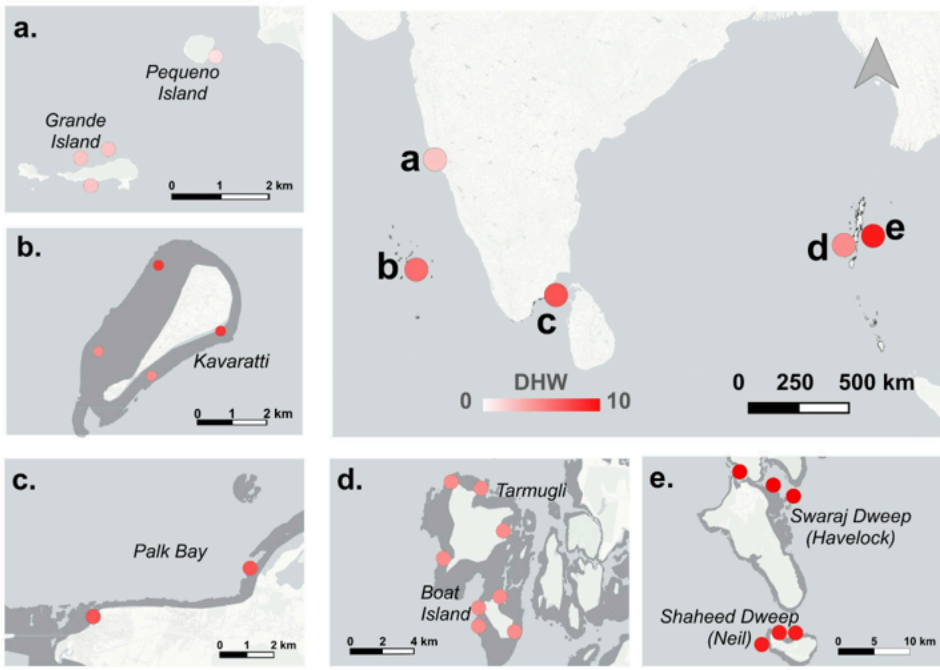

Figure 1

Map of study area with regions across the Indian subcontinent, with the colour of the points indicating the average degree heating weeks at the time of sampling in each region, namely: a - Goa (Grande Island and Pequeno Island); b - Lakshadweep (Kavaratti); c - Palk Bay; d - Mahatma Gandhi Marine National Park (Boat Island and Tarmugli Island); e - Ritchie's Archipelago (Swaraj Dweep and Shaheed Dweep)

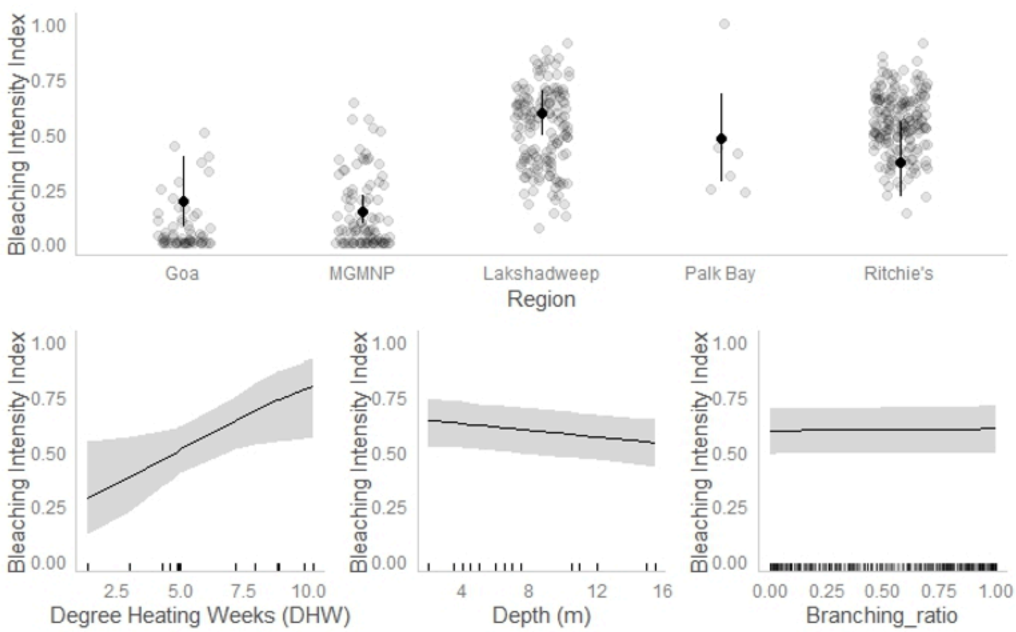

Figure 2

Model based adjusted predictions for the effect of - **a**. Region (black lines are 95% confidence intervals) **b**. Degree heating weeks. **c**. Depth **d**. Branching ratio - on BII (grey backgrounds are confidence intervals). Observations have been overlaid as translucent points in fig **2a**, and as ticks on the x axis in **2b**, **2c** and **2d**.

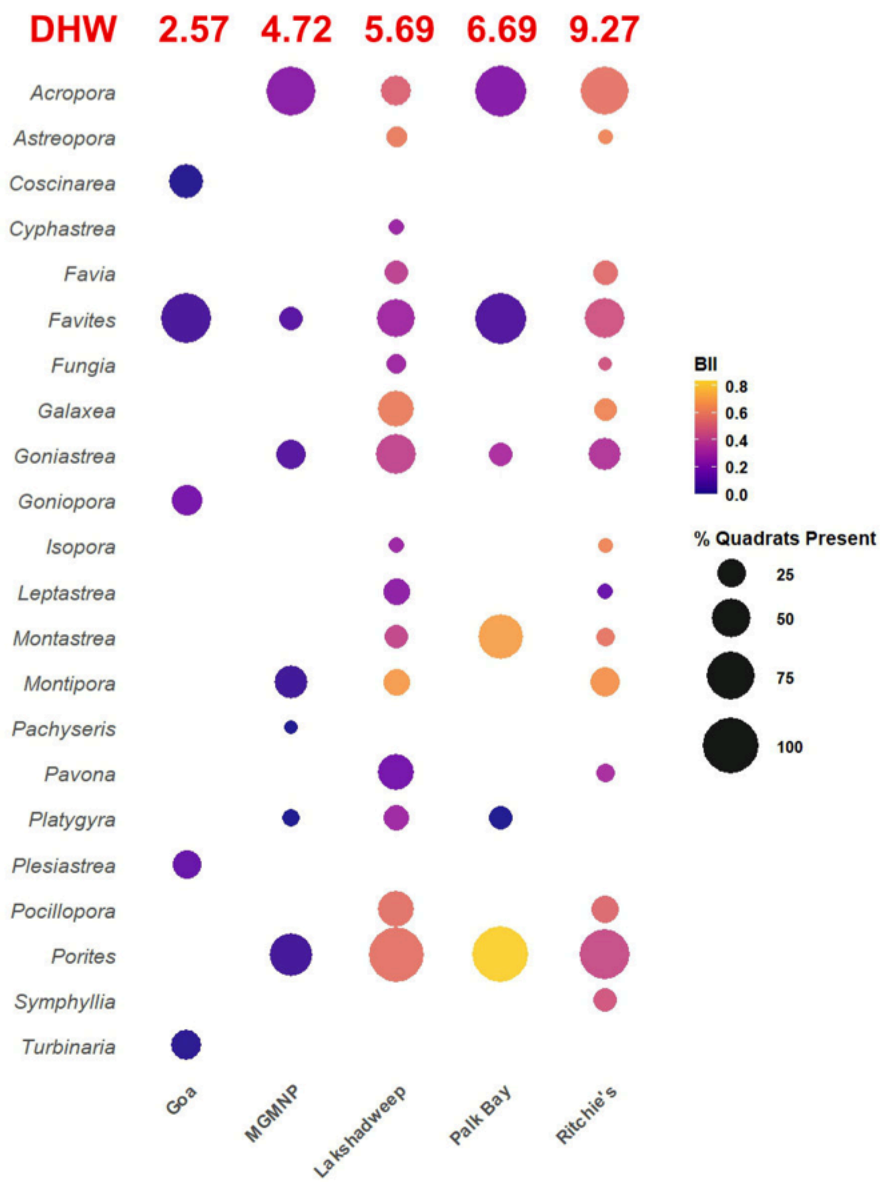

Figure 3

A matrix of the Bleaching Intensity Index of each genus across each Region. Regions are marked on the x axis in order of the mean DHW values at the time of sampling, while genera are on the y axis. The numbers on the top indicate the average heat stress values for each region at the time of sampling. The colour of the circles indicates the BII while their size reflects the ubiquity of each genus within the region; Larger circles indicate presence in a greater proportion of quadrats, and missing points indicate either absence or presence in less than 5% of quadrats from the Region.

Supplementary Files

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- SupplementaryMaterialRegionalandgenusspecificfactorsunderpinbleachingvariationacrossIndiascoralsreefsduringthefourthglobalcoralbleachingevent.dc